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A NEW SPECIES OF *TRIMERORHACHIS* (AMPHIBIA, TEMNOSPONDYLI) FROM THE LOWER PERMIAN ABO FORMATION OF NEW MEXICO, WITH DISCUSSION OF PERMIAN FAUNAL DISTRIBUTIONS IN THAT STATE

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ABSTRACT

A new species, *Trimerorhachis sandovalensis*, is based on a nearly complete skull and large portion of postcranial skeleton from the Lower Permian Abo Formation near Jemez Springs, north-central New Mexico. Numerous other specimens, indeterminate at the specific level, indicate that *Trimerorhachis* was distributed over a wide area of New Mexico during the Early Permian. Paleogeographic reconstructions of New Mexico at that time suggest that *Trimerorhachis*, as well as the lungfish *Gnathorhiza*, rhipidistian crossopterygian fishes, the amphibian *Diplocaulus*, and the reptile *Dimetrodon*, were inhabitants of a wide coastal plain that extended from shallow marine environments along the southern margin of the state to highlands along the northern margin of the state. These "coastal plain" inhabitants are absent from contemporaneous, highly fossiliferous beds of the Lower Permian Cutler Formation at Arroyo de Agua and El Cobre Canyon deposited adjacent to the northern highlands, only 45 km north of Jemez Springs. The Arroyo de Agua and El Cobre Canyon faunas, in turn, include many forms not found as yet in the region of the "coastal plain" of New Mexico.

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INTRODUCTION

At the time of Langston's (1953) detailed account of the Lower Permian amphibians of New Mexico, *Trimerorhachis* remained unrecorded from the state even though it is one of the most common animals of the Lower Permian of Texas and Oklahoma. Langston viewed the absence of this amphibian in New Mexico as quite unusual because the Lower Permian vertebrate faunas of New Mexico and Texas are in general similar. He considered it improbable that this apparent anomaly was due to sampling error or the result of unfavorable climate, physical environment, or differences in food supply. What was known at that time about the Early Permian vertebrates of New Mexico was based primarily on excellent collections from the fairly restricted but intensively prospected exposures of the Cutler Formation near Arroyo de Agua and in El Cobre Canyon, which lie only about 30 km apart in north-central Rio Arriba County. Collections from the very extensive Lower Permian exposures of the remainder of the state, particularly the Abo Formation, were small and fragmentary. Only in recent years have these relatively neglected exposures received careful attention, with the result that it can now be stated that *Trimerorhachis* was probably a common element of the fauna outside of the Arroyo de Agua-El Cobre Canyon collecting region.

Olson and Vaughn (1970) were the first to report *Trimerorhachis* from the Lower Permian of New Mexico. This was based on a partial skull from the Abo Formation of the Caballo Mountains in south-central Sierra County. The specimen described here as a new species, *T. sandovalensis*, was collected from the Abo Formation near Jemez Springs, Sandoval County, in north-central New Mexico. At least four other undescribed, partial skulls from the Abo Formation of New Mexico can now be assigned to this genus, but without specific designation. Three of these specimens are from two localities that are roughly equidistant between Jemez Springs and the Caballo Mountains, indicating that *Trimerorhachis* was wide ranging in New Mexico during the Early Permian.

Recent papers by Vaughn (1966b, 1969b, 1970) have helped greatly in understanding distribution patterns of Early Permian vertebrates throughout the Southwest. New faunal discoveries in New Mexico, however, necessitate changes in his model which is based on paleogeographic reconstructions. A tentative explanation is offered for the absence of *Trimerorhachis* from the Lower Permian Cutler exposures of the Arroyo de Agua-El Cobre Canyon region in north-central New Mexico and its seemingly common occurrence in the extensive Abo exposures of central and south-central New Mexico.

The following abbreviations are used to refer to repositories of specimens: AMNH, American Museum of Natural History, New York; CM, Carnegie Museum of Natural History, Pittsburgh; FMNH, Field Museum, Chicago; YPM, Peabody Museum of Natural History, Yale University, New Haven.

SYSTEMATIC PALEONTOLOGY

Class Amphibia

Subclass Labyrinthodontia

Order Temnospondyli

Family Trimerorhachidae

Genus *Trimerorhachis* Cope 1878

Trimerorhachis sandovalensis, new species

Holotype.—CM 38025 is a partial, articulated skeleton preserved on three separate blocks. The nearly complete skull with closely adhering lower jaws, first eight presacral vertebrae with many ribs fairly well represented and most of pectoral girdle are preserved in a single block in nearly perfect articulation. On another block an isolated string of three vertebrae with rib fragments, exhibiting some displacement and crushing of individual elements, is believed to be from the posterior region of the dorsal column. A third small block contains closely associated or loosely articulated skeletal elements of the pelvic region. These include: last five or six neural arches and three intercentra of posteriormost dorsal vertebrae, ilia and ischia, proximal end of left femur, first five or six caudal neural arches, and a few scattered complete and fragmentary ribs belonging to caudal and dorsal series of vertebrae.

Horizon and locality.—Lower part of Abo Formation, Wolfcampian, Lower Permian, on west side of Canyon de San Diego, west of State Highway 4 and along western edge of Jemez River, about 11.5 km south of Jemez Springs, approximately lat 35°40'N and long 106°45'W, Sandoval County, New Mexico. CM 38025 was collected from a thick sequence of light red mudstones. The specimen, however, was directly surrounded by poorly consolidated, coarse-grained, light gray sediments of a very small stream channel lens. Some unidentifiable vertebrate fragments were also found weathered-out of this lens.

Diagnosis.—A trimerorhachid labyrinthodont assignable to the genus *Trimerorhachis* based on the presence of large postorbital and lacrimal that restricted greatly or eliminated the contribution of the jugal to the orbital margin. The following features distinguish *Trimerorhachis sandovalensis* from other species of this genus: small, posteriorly directed, triangular process of premaxilla penetrates anterior margin of nasal just medial to external naris; prefrontal lacks a distinct, narrow, posterior process that would extend along anterior half of

medial border of orbit; prefrontal has very narrow, transverse contact with anterior process of postfrontal; intertemporal is diamond-shaped and its anterior end deeply penetrates posterolateral margin of postfrontal; jugal may have a small contribution to orbital margin; quadratojugal extends anteriorly only to about level of anterior border of postparietal and jugal in turn is relatively longer posteriorly. Lateral halves of atlantal intercentrum appear fused to neural arch pedicels to form ventral laminae that surround both neural and notochordal canals and meet, or nearly meet, at ventral midline of column; atlantal pleurocentrum is either absent or represented only by a very small, lens-shaped, inclusion along posterior margin of ventral lamina of neural arch. In neural arches 2 through 8 spines are well ossified and exhibit no fore and aft grooves that would mark their midline union as lateral halves, and posterior, as well as anterior, zygapophyses and transverse processes are well developed; anterior dorsal ribs taper smoothly to their distal end rather than expand. Scapula possesses a deep, V-shaped cleft that extends anteriorly from upper half of its posterolateral margin.

Etymology.—From Sandoval County.

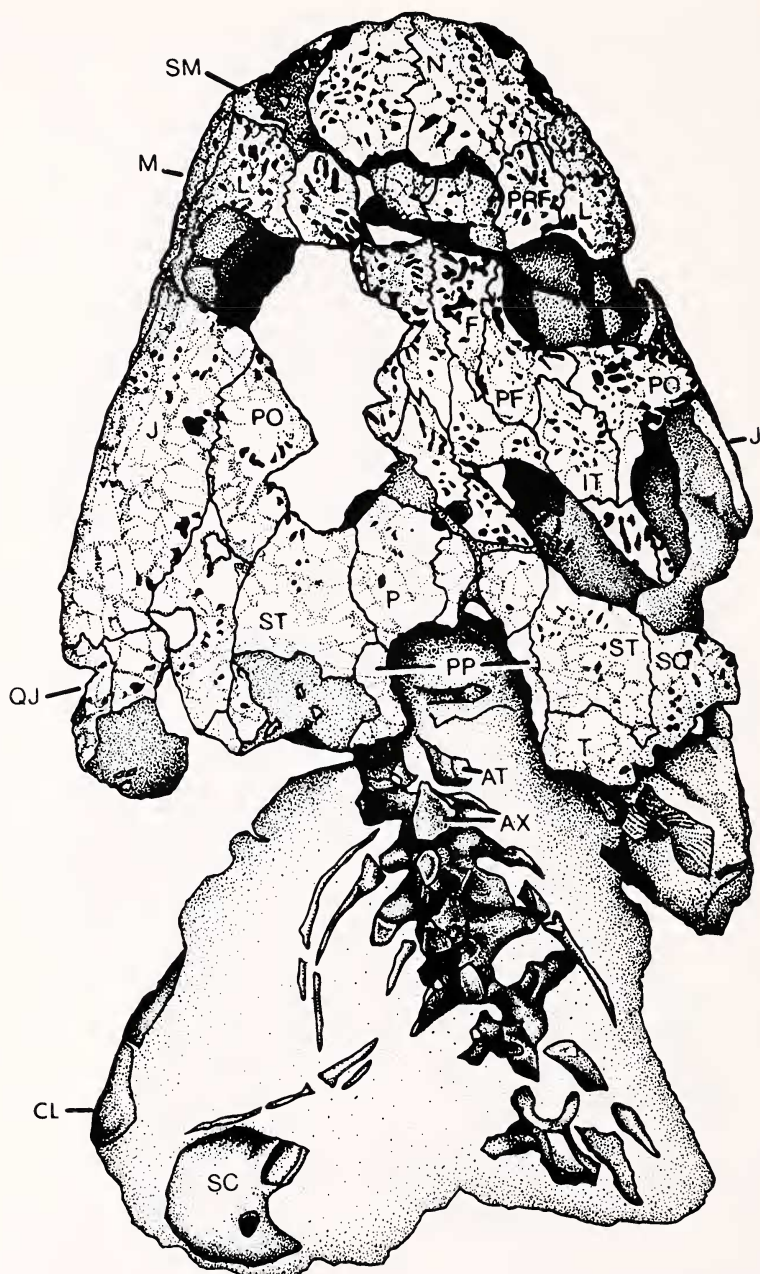
Description

Skull and lower jaw.—Case (1935) gave a fairly detailed account of the skull, lower jaw, and much of the postcranial skeleton of *Trimerorhachis*, probably *T. insignis* (Olson, 1955). The following description of the skull (Figs. 1–6) is therefore limited to features that distinguish *T. sandovalensis* from other species of this genus. Some dorsal crushing in the interorbital region of the skull has displaced slightly the frontals, and inward crushing of the right ventrolateral margin has reduced or eliminated the dorsal exposure of the roofing bones in this region. Undistorted the skull was bluntly arrow-shaped with an estimated midline length of about 10.0 cm and greatest width of approximately 10.5 cm. Though the posterior margin of the skull roof is incomplete, the otic notch was undoubtedly shallow, as is typical of *Trimerorhachis*. The orbit is sub-round in outline with its long axis, about 1.7 cm, directed toward a point midway between the nares. The oval narial opening is of moderate size, with a greatest diameter of about 1.0 cm, and faces dorsolaterally and slightly anteriorly. Much of the surface texture of the roofing bones has been lost due to weathering and preparation. The remaining sculpturing consists mainly of circular pits which in some areas become elongated grooves arranged in a radiating pattern. None of the lateral line grooves of the skull roof can be detected. A restoration of the skull roof in dorsal view is given in Fig. 5.

Only a small posterolateral portion of the right premaxilla remains. It was undoubtedly only narrowly exposed dorsally and formed the anterior and ventral borders of the external naris. None of the premaxillary teeth remain. The nasal exhibits a small but distinct V-shaped notch on its anterior margin just medial to the naris that was obviously occupied by the premaxilla. The septomaxilla lies within the plane of the skull surface, is sculptured, and forms the posterior margin of the naris, excluding the lacrimal and maxilla from this opening. It is roughly crescent-shaped, with the upper half of the crescent thinning greatly along its lacrimal contact. The right septomaxilla has been displaced slightly anteroventrally. The prefrontal makes only a very small contribution



Fig. 1.—*Trimerorhachis sandovalensis*, holotype, CM 38025: photograph showing skull and first seven vertebrae with ribs in dorsal view and left scapula in lateral view.



to the anteromedial margin of the orbit. This is due in part to a short, thin process of the lacrimal that projects medially along the orbital rim. The postfrontal forms essentially the medial margin of the orbit; anteriorly it has a narrow, transverse suture with the prefrontal. Posterolaterally the postfrontal is penetrated by the anterior end of the diamond-shaped intertemporal bone; a small laterally directed process of the postfrontal thus forms part of the posterior orbital margin. Neither jugal is complete and it cannot be determined directly whether it entered the orbit or was excluded by a lacrimal-postorbital contact. The disposition of the left jugal-postorbital suture does suggest, however, that the jugal may have made a small contribution to the orbit. The anterior end of the preserved portion of the jugal-postorbital suture swings abruptly anteromedially to within a few millimeters of the estimated position of the orbit and its intersection with the orbital rim would appear to have been likely. The quadratojugal-jugal contact is positioned at about the level of the anterior border of the postparietal. Both maxillae appear to be complete and are only narrowly exposed in dorsal view. The maxilla has only a narrow contact with the septomaxilla, exhibits a slight, vertical expansion just posterior to the naris, then tapers steadily posteriorly to a point. The maxillary dentitions are preserved mainly as an incomplete series of impressions; only the impressions of the teeth of the posterior halves of the series are complete. The teeth are simple, sharply pointed pegs which increase gradually in size anteriorly, where they reach a maximum length of about 4 mm. The maxilla held approximately 45 teeth.

The lower jaws are firmly attached to the skull, making it impossible to expose the palate or the jaws completely. What can be seen of the left side of the palate is depicted diagrammatically in Fig. 6. All of the elements of the palate are essentially complete except the pterygoid. Partial loss and distortion prevents description of the quadrate wing of the pterygoid and the region of the basicranial articulation. The pterygoids and vomers form the lateral borders of a wide interpterygoid vacuity. The pterygoid is covered by a shagreen of denticles except for a narrow margin along its contact with the vomer and possibly with the ectopterygoid and palatine. The ectopterygoid and palatine are narrow and carry a row of 12 sharply pointed teeth; these are slightly recurved medially. There are spaces for three more teeth. Anteriorly the series begins with a socket-and-tusk pair. The tusk is about 11 mm long and is much larger than the other tusks. Teeth 3 through 11 increase in length posteriorly from about 3.5 mm to about 7 mm and the last four teeth are equal in size with a length of about 4 mm. The ectopterygoid bears the last five or six teeth of the series. The vomer is large and terminates posterolaterally as a V-shaped wedge between the anterior ends of the pterygoid and palatine. At the anteromedial corner of the vomer is an anterior palatal fenestra that accommodates the large parasymphysial tusk of the lower jaw; the exact dimensions of this opening cannot be determined. The vomer forms the medial border of the internal naris; the lateral border of the internal naris is not visible but it is likely that the palatine entered its posterolateral margin. A semicircular notch at the posterior end of the midline union of the vomers undoubtedly received the anterior end of the

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Fig. 2.—*Trimerorhachis sandovalensis*, holotype, CM 38025, as seen in Fig. 1. Abbreviations used in figures are as follows: A, angular; APF, anterior palatine fenestra; AT, atlas; AX, axis; BO, basioccipital; CL, clavicle; D, dentary; EC, ectopterygoid; EO, exoccipital; F, frontal; FE, femur; FSGL, supraglenoid foramen; IC, intercentrum; ICL, interclavicle; IL, ilium; IN, internal naris; IS, ischium; IT, intertemporal; J, jugal; L, lacrimal; M, maxilla; N, nasal; P, parietal; PC, pleurocentrum; PF, postfrontal; PL, palatine; PM, premaxilla; PP, postparietal; PRC, precoracoid; PRF, prefrontal; PRO, proatlas; PS, parasphenoid; PSP, postsphenial; PT, pterygoid; QJ, quadratojugal; SA, surangular; SC, scapula; SM, septomaxilla; SP, splenial; ST, supratemporal; T, tabular; V, vomer.



Fig. 3.—*Trimerorhachis sandovalensis*, holotype, CM 38025: photograph showing skull with lower jaws, portion of braincase and pectoral girdle in ventral view.

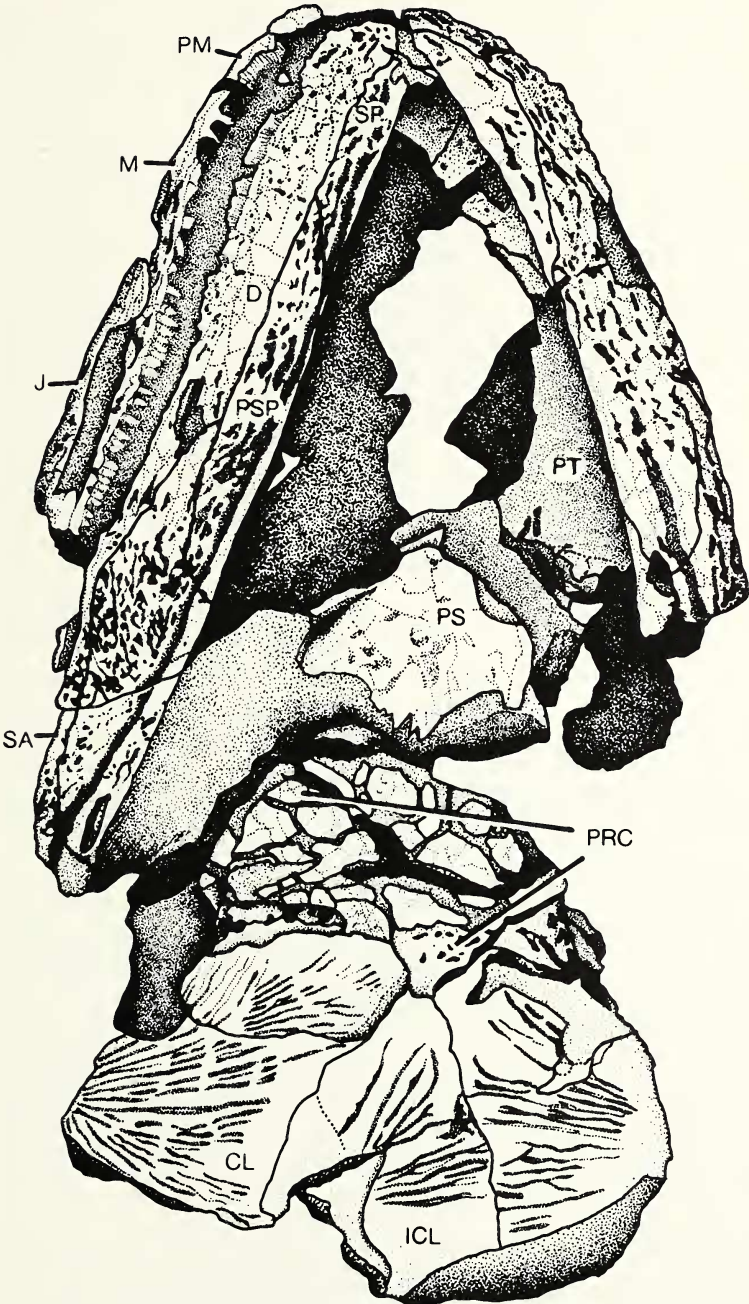


Fig. 4.—*Trimerorhachis sandovalensis*, holotype, CM 38025, as seen in Fig. 3.

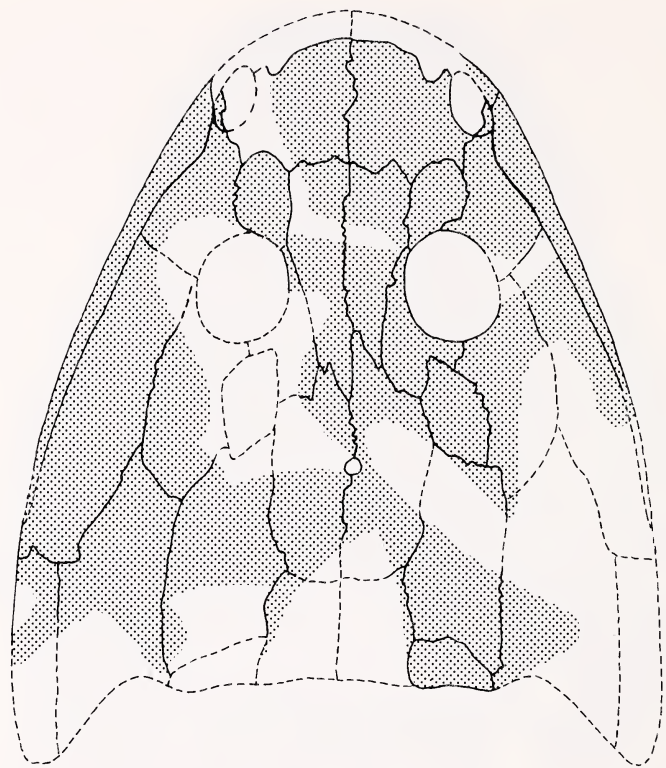


Fig. 5.—Diagrammatic restoration of skull roof of *Trimerorhachis sandovalensis* in dorsal view. Preserved areas represented by stippling.

cultriform process of the parasphenoid. Three distinct groups of teeth are found on the vomer. A transverse, tightly grouped row of five, sharply pointed teeth, about 3 mm in length, are seen just posterior to the anterior palatal fenestra. Immediately anterior to the internal naris is a tusk-and-socket pair similar in size and form to that at the anterior end of the palatine. One needle-like tooth about 2 mm in length and the bases of two more are positioned along the anteromedial margin of the internal naris.

The right lower jaw is complete but the posterior third of the left is missing; it has not been possible to expose either the dorsolateral margin, the marginal dentition, or the posteromedial surface in the region of the adductor fossa. Features of the exposed regions of the jaws are, in general, well preserved and exhibit no significant differences from the description given by Case (1935). Of the areas exposed, only the coronoid series cannot be seen in the accompanying figures and, therefore, requires some comment. The posterior coronoid extends anteriorly to the level of the anterior end of the prearticular. The lateral two thirds of its surface bears numerous denticles which appear to be arranged roughly into three longitudinal rows that converge and become indistinguishable at the anterior end of the bone. The intercoronoid has two clusters of small teeth: one contains about six teeth, the largest less than a millimeter in length, and is positioned at its posteromedial border; the second, about a dozen teeth, ranging in size from minute denticles to almost 3 mm in length, lies at its middle. Six incomplete teeth

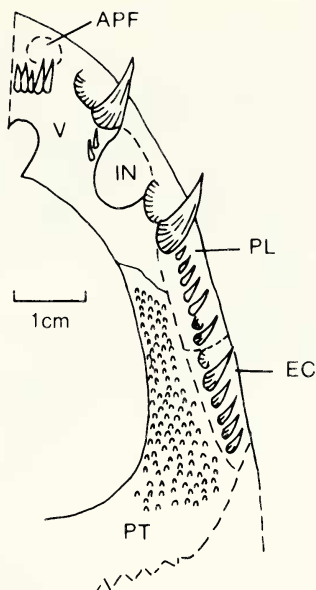


Fig. 6.—*Trimerorhachis sandovalensis*, holotype, CM 38025. Diagrammatic sketch of palate.

with maximum lengths probably about 2 mm are arranged in a longitudinal row on a slightly elevated base at the middle of the precoronoid. Immediately posterior to these teeth is a slight depression in the precoronoid that probably accommodated the distal end of the large tusk-like tooth that projects downward from the anterior end of the palatine. Anterior to the precoronoid is a deep, basin like depression along the splenial-dentary suture into which the large vomerine tusk from the anterolateral border of the internal naris probably extended. The splenial makes a small contribution to the symphysis.

A short retroarticular process is continuous with the medial surface of the jaw, but is set off laterally by the mandibular lateral line groove. There is no indication in *T. sandovalensis* of an external or lateral tuberosity, separated medially from the retroarticular process by the mandibular lateral line groove that is developed to varying degrees in other species of *Trimerorhachis* (Olson, 1955). The lateral line system is almost completely preserved and easily traceable on the right jaw. The mandibular groove begins on the posterior margin of the jaw, lateral to the retroarticular process, and extends the full length of the ventromedial margin of the jaw. A dentary sensory groove branches off the mandibular groove below the articular and extends anteriorly along the angular-surangular suture; it can be followed only to where it passes under the posterior end of the dentary. It is not possible to identify the accessory groove, illustrated by Romer (1947) in *Trimerorhachis* as branching off the mandibular groove and extending a short distance anteriorly across the upper surface of the surangular just above the dentary groove.

Disarticulation and poor ossification eliminate the opportunity of a detailed examination of the braincase. The well ossified exoccipitals, only slightly disturbed, are identical with those described by Case (1935). The only visible portions of the well-ossified basioccipital are a narrow margin along the posterior border of the ventral surface of

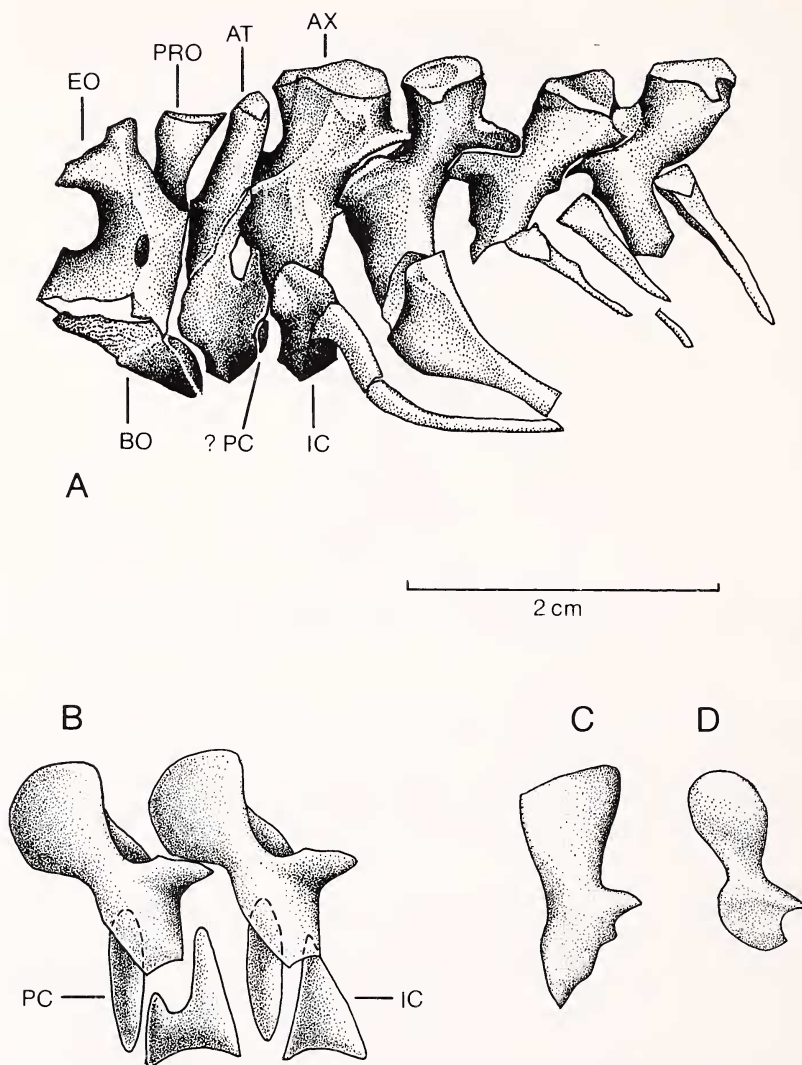


Fig. 7.—*Trimerorhachis sandovalensis*, holotype, CM 38025. A, first five vertebrae with associated ribs and portion of braincase in left lateral view; B, posterior dorsal vertebrae restored in right lateral view; C, neural spine of posteriormost dorsal vertebra restored in right lateral view; D, neural spine of anteriormost caudal vertebra restored in right lateral view.

the braincase and most of the right lateral surface. The parasphenoid, exposed in ventral view, is missing the cultriform process. The ventral surface of the smooth main body of the parasphenoid is slightly concave. Posteriorly, from the base of the cultriform process, the parasphenoid expands to form a pair of broad, lateral wings. Close to and paralleling the anterolateral border of the lateral wing is a groove (best preserved on the right) which widens and deepens as it extends posterolaterally to the edge of the bone. The anterolateral margin of the lateral wing that is set off by this groove, referred to as the articular process of the parasphenoid, apparently functioned as the cranial articular surface in the mobile joint between palate and braincase (Chase, 1965; Watson, 1956). The posterior margins of the lateral wings are strongly concave on either side of a short stem with a feathered posterior border. The posterior stem covered most of the ventral surface of the basioccipital.

Vertebrae and ribs.—The vertebral column is represented by three separate series of vertebrae that undoubtedly belong to a single individual. The first of these series is a string of eight vertebrae that are associated with the skull and pectoral girdle and in nearly perfect articulation and preservation. Parts of most of the ribs are represented and are closely associated with their respective vertebrae, some in nearly proper articulation. The second series is an articulated string of three incomplete vertebrae that are probably posterior dorsals; only a few fragments of ribs are associated with them. On a block containing the pelvic girdle and the proximal end of the right femur are about a dozen loosely associated neural arches, most of which are complete, three incomplete but articulated intercentra, as well as several complete and fragmentary ribs. On the basis of size and position relative to the pelvic girdle about half of the neural arches and the incomplete intercentra are believed to be posterior dorsals and the remaining neural arches anterior caudals; no sacral vertebrae can be distinguished nor can pleurocentra be clearly identified in this series.

The atlas-axis complex (Fig. 7a) is complete, only slightly disturbed, and nearly completely exposed except in right lateral view. The proatlas is missing and the axial pleurocentrum is covered by the pectoral girdle. The neural arch of the atlas consists of paired halves. The spine of each atlantal arch half is narrow (the left is narrower possibly because of weathering or preparation) and slightly tapered dorsally. In life it was probably directed posterodorsally across the anterior half of the axial spine, terminating slightly below the top of the axial spine. The atlantal neural arch articulates with the anterior zygapophysis of the axis by way of a flange near the posteromedial edge of the spine. Above the posterior zygapophysis the spine is subcircular in cross section. The anterior surface of the spine narrows to an edge as it extends a short distance below the level of the posterior zygapophysis, then expands somewhat to form a small but well defined anterior zygapophysis for the proatlas. This flat articular surface faces antero-dorsally and projects somewhat outward from the lateral surface of the neural arch as a thin lip. Below the level of the zygapophyses the lateral surface of the atlas is greatly expanded ventrally, first sloping steeply ventrolaterally, then gently curving medially to nearly reach the ventral midline of the column. Because this structure extends below the neural canal to surround the notochordal canal laterally and ventrally, it probably represents a fusion of the lateral half of the intercentrum with the neural arch pedicel; for purposes of description it will be referred to simply as the ventral lamina. The upper half of the lateral surface of the ventral lamina is flat, whereas ventrally it is slightly concave in horizontal section. The upper half of the anterior edge of the lamina is hidden by the exoccipital; the upper half of the posterior margin exhibits a deep oval notch that probably allowed for the exit of the spinal nerve. As the lamina approaches the ventral midline of the column it tapers to a bluntly rounded margin. As preserved, the opposing laminae approach to within 4 mm of each other ventrally; because the left neural arch has been displaced, this separation was probably negligible or nonexistent in life. A very small lens-shaped element within a shallow, well defined concave emargination of the posterior border the ventral lamina may represent a much reduced pleurocentrum. Un-

fortunately, the presence of this element on the opposite side of the column cannot be confirmed without destruction of other structures. The proatlas is a small element lying immediately anterior to the left atlantal neural spine. In lateral view, it is wedge-shaped with a truncated narrow end. As preserved its long axis is oriented vertically and the narrow end ventrally. In life the narrow end undoubtedly articulated with the anterior zygapophysis of the atlantal neural arch and the long axis was directed anterodorsally. In horizontal section the proatlas is convex laterally and flat along most of its medial surface except below, where it appears to be moderately excavated.

The axial neural arch is a single massive structure with a neural spine that is considerably larger than those of the succeeding vertebrae. In horizontal section the spine resembles an isosceles triangle with the narrow apex directed anteriorly. The summit of the spine is obviously incomplete, due most likely to weathering. There is little or no buttress support of the anterior zygapophysis and the articular surface extends only a very short distance out from the lateral surface of the pedicel as a thin lip. The lateral edge of the lip is continuous with a ridge that extends posterodorsally across the lateral surface of the spine. The posterior zygapophysis, like those of the immediately following vertebrae, is well developed with a small buttress. Without change in length the pedicel is confluent with the well developed transverse process which projects laterally and slightly ventrally without reduction in width to about 11 mm from the midline. It was not possible to expose the ventral surface, the anterior edge of the dorsal surface, or the rib facet of the process. It is clear that the transverse process is thickest along its smoothly rounded posterior edge and slowly thins toward its anterior edge, accounting for the very slight anteroventral slope of its flat upper surface. The paired elements of the axial intercentrum have an abutment contact along the ventral midline of the column. Although only the ventral half of the right element is visible, the left is nearly entirely exposed. The left element has been displaced so that its upper end lies wedged between the distal end of the axial transverse process and the proximal end of the rib that articulated with it. From the substantial midventral abutment the left element curves dorsally, thinning somewhat in anteroposterior width, and terminates in a bluntly rounded end. In end view the right and left halves of the intercentrum form a thin-walled crescent. The external surface of the left half is smooth and flat except at the dorsal end, where it appears slightly concave. The neural arches of vertebrae 3 through 8 are, for the most part, complete and well exposed; the intercentra and pleurocentra cannot be exposed because of the closely associated pectoral girdle. A wide gap between vertebrae 6 and 7 may indicate the loss of a vertebra. In general there is a serial reduction in the width of the neural spines posteriorly, which in dorsal view (Figs. 1, 2) exhibit a wide variety of outlines; spines 3 and 5 are anteroposteriorly oval, spine 4 is triangular like that of the axis, spines 6 and 7 are transversely narrow blades (spine 8 is incomplete). The tops of all the spines are poorly ossified and were probably capped or continued a short distance in cartilage; none of the vertebrae has a zone of reduced ossification delineating right and left halves of the spines. The zygapophyses are well developed with the articular surfaces tilted steeply downward and inward. The transverse processes are well developed, project directly laterally and slightly ventrally to about 9 mm from the midline and are positioned at a level just anterior to the neural spine. In cross section the processes are roughly teardrop-shaped with the rounded thickened posterior edge tapering to a thin anterior edge; the processes gradually shorten in anteroposterior width in more posterior vertebrae by retreat of the anterior edge.

In the articulated string of three posterior dorsal vertebrae the intercentra and pleurocentra have undergone some displacement and crushing; a restoration is given in Fig. 7b. The neural arches show marked differences from those of the anterior dorsal vertebrae. They consist of transversely thin right and left halves which have been slightly displaced relative to each other; it appears that in life they were joined to form a sharply keeled edge anteriorly, whereas posteriorly they diverged, being separated by either a widening wedge of cartilage or poorly ossified bone. In lateral view the spines are

smoothly rounded at their summit, taper to a narrow waist at their base, and are inclined slightly posteriorly; their lateral surfaces are very slightly concave. The anterior zygapophyses are well developed, extend out from the lateral surface of the neural arch, and the articular facet slopes moderately inward and downward. Posteriorly the lateral edge of the anterior zygapophysis continues as a prominent ridge that turns abruptly dorsally and extends for a short distance before joining the upper portion of the anterior edge of the spine. The posterior zygapophysis is weakly developed and cannot be delineated in lateral view. It is apparently immediately above the emargination that forms the anterior margin of the intervertebral notch. The transverse process is not distinct. The flat, lateral surface of the pedicel is continued smoothly ventrally and slightly anterolaterally, narrowing somewhat in width. Distally it ends in a longitudinal oval rib facet. In end view the intercentra are very thin-walled half rings, opening dorsally. Ventrally they are wide anteroposteriorly and in most the lateral ascending processes taper to a point dorsally, giving the intercentra a wedge-shaped appearance in lateral view. The anterior and posterior borders of most of the ascending processes are straight; there are two exceptions, however. In the three consecutive intercentra the anterior borders of the left ascending processes are concave. The posterior borders of two consecutive right lateral ascending processes have a fairly deep, vertical notch that creates a secondary posterior process that is much lower and somewhat narrower than the primary process; the notch probably marks the point of articulation of the rib capitulum. The outer surfaces of the intercentra are slightly concave. Randomly scattered pits on their outer surface may indicate incomplete ossification. Only one of the pleurocentra, a right, is completely exposed laterally. It is lozenge-shaped with a height about four times its length. The height of the pleurocentrum is about equal to that of the adjacent intercentra, but it undoubtedly occupied a more dorsal position in the column. The pleurocentrum exhibits little or no curvature around the notochordal canal and its lateral surface is only very slightly concave. Surface sculpturing is limited to a few scattered pits. No facet for the rib articulation can be recognized.

The five or six posterior dorsal neural arches (Fig. 7c) associated with the pelvic girdle exhibit a number of differences from the other dorsal neural arches. The neural arches are not separated into lateral halves and their flat lateral surfaces meet in a sharp anterior edge. A narrow triangular space between the periosteal bone layers of the spines was probably occupied by cartilage. In lateral view the spines are narrower toward their base, terminate dorsally in a plane that slopes somewhat posteroventrally, and are inclined backward. The anterior zygapophyses are weakly developed and do not project noticeably out from the lateral surface of the neural arch. The posterior zygapophyses are not discernable and probably occupied the same apparent position as those of the other posterior dorsals. The lateral surfaces of the pedicels are flat, and narrow somewhat ventrally. The distal and anterior edges of the pedicel are thin and not well defined; the portion that forms the posterior border of the intervertebral notch below the anterior zygapophysis is well ossified. The bases of the three consecutive intercentra are closely associated with the posteriormost dorsal neural arches; they are identical to those of the probable posterior dorsals. The halves of the anterior caudal neural arches (Fig. 7d) are weakly joined in the sagittal plane and are displaced slightly along their midsagittal union. These neural arches are comparable to those of the posteriormost dorsal vertebrae. In lateral view the neural spines are, however, rounded at their summit and deeply waisted at their base; the latter feature becomes more pronounced posteriorly in the series. The pedicels are less developed than in the presacral vertebrae, terminating in a smoothly convex margin at the intervertebral notch.

Ribs are closely associated with vertebrae 2 through 6; the atlas lacks a rib. Some of the ribs are complete, but in most the shafts are incomplete. It has not been possible to expose fully any of the ribs. The axial rib (25 mm long) is distinct from the successive dorsal ribs; it is strongly curved posteriorly with most of the curvature occurring at its midlength. The rib is vertically oval in cross section. In greatest diameter it tapers

smoothly from 3 mm at its proximal end to about 1 mm at midlength. The shaft of the rib with the third vertebrae is 26 mm long, is oval in cross section, and is gently curved posteriorly. The proximal end is greatly expanded vertically, forming a triangular head that tapers distally from about 1 cm to about 3 mm in a distance of 1 cm. There is no constriction of the head into separate capitulum and tuberculum portions. All of the ribs associated with the anterior vertebrae appear to taper distally. There are four ribs associated with the posteriormost dorsal vertebrae, but only two are well enough preserved or exposed to allow comment. One is 1.5 cm long and is moderately curved, the convex margin probably representing the lateral or anterior surface of the rib. The shaft appears to be oval in cross section, at least along its proximal half, with its greatest diameter between the concave and convex margins. In this dimension the rib tapers smoothly distally from 4 mm at its proximal end to 1.6 mm in a distance of 5 mm, then slowly expands again to 2 mm at about two thirds its length before again tapering to a distal point. The proximal 3 mm or so of the rib exhibits a noticeable dorsoventral thickening of its concave margin to accommodate an expanded articular facet that is teardrop-shaped in outline with the apex formed by the convex margin of the rib. The second rib found with this series of vertebrae is poorly preserved and only its outline can be seen. It is greatly curved, measures 2.5 cm in length and 3 mm across the proximal end, and tapers gradually to its pointed distal end. The head is badly fractured. This rib could also belong to one of the anterior caudal vertebrae.

Appendicular elements.—The preserved portions of the shoulder girdle include the clavicles, interclavicle, left scapula, and what is tentatively identified as an unpaired, median precoracoid. The clavicles and interclavicle (Figs. 3, 4) are exposed externally and are firmly articulated. The interclavicle is incomplete posteriorly, but what remains does not differ noticeably from that of other *Trimerorhachis* species. The exposed surface is in general diamond-shaped; the area of the interclavicle formed by the anterior angle far exceeds that of the posterior angle. Anteriorly the interclavicle does not quite extend to the level of the anterior edges of the clavicles. Posteriorly, it extends a short distance beyond the posterior borders of the clavicles. Surface sculpturing consists mainly of ridges and grooves that radiate from an area on the midline about one third the length of the bone from its posterior end. The clavicles have the usual form. They consist of a broad triangular, horizontal plate in ventral view; the anterolateral margin becomes increasingly curved dorsally toward the nearly transverse posterior border of the clavicle, where the posterolateral corner is directed at nearly a right angle to the rest of the bone. The entire external surface is ornamented by ridges and grooves, occasionally anastomosing, that radiate from a center near the posterolateral corner. There is no distinct ascending process at the posterolateral corner of the clavicle.

The left scapula is exposed in lateral view (Figs. 1, 2). The posterior margin is deeply concave and from this border the scapula is greatly expanded anteriorly as a roughly semicircular plate. Along the upper half of the posterior margin is a deep, V-shaped cleft which extends to the dorsal edge of the bone. In horizontal section the walls of the cleft, which are of smoothly finished bone, converge anteriorly. All but a small ventral portion of the posterior edge of the inner wall of the cleft forms nearly the entire upper half of the posterior margin of the scapula. This portion of the concave posterior margin of the scapula is extremely thin; ventrally, however, it widens steadily and substantially and has a very slightly convex surface. There is no indication that the thickened, posteroventral corner of the scapula contributed to the glenoid fossa. The lower third of the scapula is pierced by a large oval supraglenoid foramen.

Ventral view of the shoulder girdle shows a large, for the most part flat, unpaired, median element, composed mainly of a mosaic of narrowly separated, irregular plates of bone, that contacts most of the anterolateral margins of the clavicles and the anterior end of the interclavicle; it is tentatively identified here as a precoracoid. Although a large portion of its right posterolateral region is missing, the bone was obviously bilaterally symmetrical. The anterior border is strongly convex and from a greatest length

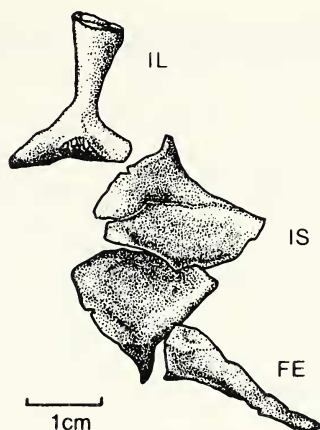


Fig. 8.—*Trimerorhachis sandovalensis*, holotype, CM 38025. Ischia (left above) in external view, left ilium in lateral view and proximal portion of right femur in dorsolateral view. Shown as preserved on a small block but without associated dorsal and caudal vertebrae and ribs.

along the midline it narrows to form right and left, posterodorsally and slightly laterally directed, pointed, wing-like structures. These extend along the anterolateral margins of the clavicles to within about 1.5 cm of their posterolateral corners. A short, roughly triangular process projects posteriorly between the anteromedial corners of the paired clavicles to contact the anterior end of the interclavicle. The right clavicle has been displaced slightly medially and posteriorly relative to the rest of the dermal shoulder girdle and reveals along its anterior margin a shallow, step-like continuation of the precoracoid posteriorly onto the dorsal surface of the clavicle. The posterior extent of the ossified precoracoid on the dorsal surfaces of the clavicles and the interclavicle cannot be determined without destruction of other elements.

The ischia and ilia (Fig. 8) are preserved; the pubes were apparently cartilaginous and as in other *Trimerorhachis* species were not preserved. Both ischia are exposed showing their ventrolateral or external surfaces; it is assumed that in life the wide, plate-like ischia sloped ventromedially towards their symphysis. The superior border is slightly concave; from this margin the ischium is expanded ventromedially as a somewhat elongated, semicircular plate. The edge of the superior border is rounded in finished bone. Only the anterior portions of the convex margins of the ischia are exposed; they are roughly finished, indicating a continuation in cartilage, as is probably the case for the entire convex margin. The inferior and superior edges thicken toward their anterior junction with each other; the remaining edge of the bone appears to be very thin. The external surface of the ischium is slightly concave. The ossified portion of the ischium did not participate in the acetabulum. Both ilia are exposed in lateral view, but only the left is seen in Fig. 8. The triangular acetabular base of the ilium is continued dorsally in a blade that expands smoothly anteroposteriorly. The dorsal edge of the blade is rough and slightly concave, indicating a cartilaginous cap or extension. The lateral surface of the acetabular base is slightly concave, as is the central area of its ventral margin. The unfinished articular surface of the acetabulum is semicircular in outline; its convex dorsal margin projects slightly outward from the lateral surface of the bone.

Of the limb elements, only the proximal half (about 2 cm) of the right femur is preserved; it is closely associated with the right ischium (Fig. 8) and is exposed in antero-

dorsal view. From an anteroposterior proximal width of 1.2 cm the head narrows in a distance of 1.5 cm to a subcylindrical shaft about 4 mm in diameter. The proximal articular surface is rough and slightly concave.

Comparison

In 1955, Olson published a revision of *Trimerorhachis* in which the number of previously named species was reduced from six to two—*T. insignis* and *T. mesops*—and a new species, *T. rogersi*, was recognized. These three species essentially follow one another in time and exhibit a stratigraphic range that is without major break from near the base of the Wichita Group up through the Clear Fork Group, the lowermost two groups of the Lower Permian section of north-central Texas. *Trimerorhachis insignis* is also common in beds of equivalent age in Oklahoma (Olson, 1967). As pointed out by Olson (1955:272), probably the most obvious feature of the history of *Trimerorhachis* is its “persistence of morphology over a rather long period of time in which there were marked changes in both the physical and biological environment.” Olson (1955) relied primarily on skull proportions in his revision of the genus, rejecting previously used characters of the lower jaw and vertebrae, as well as some proportions of the skull. In his revised diagnoses all of the characters of the skull used are given as relative differences in proportions between species and not as absolute numerical values. This prevents direct comparisons between the New Mexico species and those of the Midcontinent. Fortunately, however, the skull and postcranial skeleton of *T. sandovalensis* exhibit a number of features that set it widely apart from the others, which show strong conformity in structure. Before describing these differences it is necessary to eliminate a potential source of confusion that might arise from Olson’s (1955) diagrammatic representation of the skull of *Trimerorhachis* and illustrations of the skull of *T. rogersi*. Olson illustrated two skulls in which the sutures are indicated, the type (FMNH-UR 138; Fig. 100D, p. 264) and a referred specimen (FMNH-UR 76; Fig. 101B, p. 265). Only a few of the sutures of the posterior region of the type skull are shown and these do not appear to differ from the pattern expected in *Trimerorhachis*. The sutural pattern shown on the nearly complete, well preserved skull of the referred specimen is, however, different from that described by any other author for this genus. The most striking examples of its departure from the usual *Trimerorhachis* sutural pattern include: 1) intertemporal absent and its usual position occupied by a lateral lappet of the parietal; 2) frontal forms much of the medial orbital margin, separating the prefrontal and postfrontal from contact; 3) jugal forms most of the ventral orbital margin, greatly reducing the contribution of the lacrimal to the orbit. These and other less obvious differences of *T. rogersi* from the familiar sutural pattern of the genus are also seen in Olson’s

diagrammatic illustration of the skull of *Trimerorhachis* (Fig. 91, p. 235) in which he indicates the various measurements used in his study. Olson did not comment on these significant differences. Examination of specimens FMNH-UR 138 and FMNH-UR 76 shows that their sutural patterns are essentially the same as that of the well known *T. insignis* (Case, 1935) with one possible exception. In the smaller skull FMNH-UR 76, measuring 44 mm in midline length, the intertemporal bone is much smaller than usual in larger specimens; the larger, type skull FMNH-UR 138, about 115 mm in midline length, the intertemporal (not shown in Olson's figure) is of expected size. This relative size difference might reasonably be explained as the result of the onset of regional growth acceleration at a later stage of development. Because there appears to be no marked differences between the midcontinental species of *Trimerorhachis*, other than the proportional differences noted by Olson (1955), the well described *T. insignis* (Case, 1935) provides much of the basis for distinguishing *T. sandovalensis*.

In *T. sandovalensis* the small, posteriorly directed, triangular process of the premaxilla that penetrates the anterior margin of the nasal just medial to the narial opening is not seen in any figured specimen of the three midcontinental species. In contrast to *T. insignis* and *T. rogersi* (*T. mesops* is very inadequately known) the prefrontal of *T. sandovalensis* does not possess a distinct, narrow, posterior process that forms a substantial portion of the medial rim of the orbit. In addition, the prefrontal-postfrontal contact in *T. sandovalensis* is a very narrow, transverse suture, whereas in at least *T. insignis* the prefrontal forms a more extensive, oblique contact with the anteromedial edge of the anterior process of the postfrontal. In the midcontinental species the intertemporal is a roughly pentagonal bone that does not extend anteriorly as a wedge into the postfrontal; in *T. sandovalensis*, however, the intertemporal is diamond-shaped and its anterior end extends as a wedge into posterolateral margin of the postfrontal. Septomaxillae, which are clearly seen in the New Mexico form, have not been identified in any of the midcontinental forms except possibly in one instance. Huene (1913) identified what he believed to be a septomaxilla in the type of *T. mesops* (AMNH 4568). It was shown as a roughly triangular bone with a broad contact with the posterior border of the naris and an anteriorly directed apex. This element is quite different in outline from the septomaxilla seen in *T. sandovalensis*, raising some doubt about Huene's identification. Case (1935) was not able to identify a septomaxilla in any of the well preserved specimens of *T. insignis* he examined. One of the diagnostic features of *Trimerorhachis* is the exclusion of the jugal from the orbit by the contact of the lacrimal and postorbital. As already shown, there is some reason to suspect that in the New Mexico species the jugal may have had a small entrance into

the orbital rim. In *T. sandovalensis* the quadratojugal is rather short in anteroposterior length, extending only to the level of the anterior border of the postparietal, and consequently the jugal is long. A similar pattern is seen in early sketchy descriptions of *T. insignis* by Broom (1913:Fig. 10), Case (1911:Fig. 36), and Williston (1914:Fig. 2; 1915:Fig. 1). In Case's (1935) thorough description of an excellent series of skulls of this species the quadratojugal has an anterior extent equal to those of the squamosal and supratemporal bones, reaching nearly to the level of the pineal foramen, and the jugal is correspondingly shorter.

The presacral vertebrae of *T. sandovalensis* exhibit some obvious differences from those of the midcontinental species. The structure of the atlas is different not only from that described for this genus, but other rhachitomous amphibians in which it is known. The atlas-axis complex in the type of *T. insignis* (AMNH 4565) is well preserved, exhibits the expected complement of elements, except the proatlas, and possesses no unusual features (Case, 1911). In *T. sandovalensis* the atlas consists only of a pair of large neural arch halves with associated proatlases and possibly a pair of much reduced pleurocentra; there is no discrete intercentrum. The pedicels of the atlantal neural arches are unusual in extending to, or very nearly to, the ventral midline of the column as broad laminae that enclose both the neural and notochordal passages. In *T. insignis* the pedicels enclose only the neural canal. It is suspected that in *T. sandovalensis* the pedicel of each neural arch half has fused with the lateral half of the intercentrum to form a much enlarged structure, referred to here as the ventral lamina. The possibility of such a combination is made plausible because the axial intercentrum of *T. sandovalensis* is divided into lateral halves and Case (1911) has also noted a midline division of the first three intercentra in a specimen of *T. insignis*. In the New Mexico species it also appears that the atlantal pleurocentrum has either been lost or greatly reduced developmentally; it may be represented by the small inclusion noted along the posterior margin of the ventral lamina of the atlantal neural arch. Posteriorly from the atlas the vertebrae of *Trimerorhachis* show little regional variation (Case, 1935). The only post-atlantal vertebrae of *T. sandovalensis* that show strong deviations from the basic *Trimerorhachis* pattern are vertebrae 2 through 8. In contrast to the condition in the midcontinental species, the neural arch halves of these vertebrae in the New Mexico species are firmly co-ossified and there are no grooves on the anterior and posterior surfaces of the spines to mark their midline union. In *T. sandovalensis* both the posterior and anterior zygapophyses of vertebrae 2 through 8 are well developed and, therefore, differ from the typical *Trimerorhachis* condition in which, as noted by Case (1935), there are well developed

anterior zygapophyses, but the posterior zygapophyses are no more than a suggested area of articulation at the base of the posterior margin of the neural spine. In addition, vertebrae 2 through 8 of *T. sandovalensis* possess well developed transverse processes, whereas the entire vertebral column of the midcontinental forms is characterized by the lack of discrete transverse processes; it is presumed that the rib tuberculum of the midcontinental species articulated with the ventrolateral margin of the neural arch pedicel. Williston (1916) and Case (1935) indicated that the shafts of the anterior dorsal ribs of *Trimerorhachis* widen distally; in contrast to this condition the corresponding ribs of *T. sandovalensis* appear to taper smoothly to their distal end.

The deep, V-shaped cleft that extends anteriorly into the scapula from the upper half of its posterolateral margin is a feature not noted in any other amphibian as far as we are aware. An ossified precoracoid, or an anterior ossification of the coracoid of any kind, has also not been reported in any fossil amphibian to our knowledge, although it was undoubtedly present in most, if not all, forms as a cartilaginous structure. Paired, cartilaginous, anteromedian precoracoids are present in living amphibians and reptiles, and Miner (1925) has given convincing evidence for restoring them in the shoulder girdle of *Eryops*.

DISCUSSION

The limited outcrops of Abo Formation in the vicinity of Jemez Springs first attracted attention in the 1930's. Initial collections were made by A. S. Romer in 1931, and in 1938 a University of California, Berkeley, party made further collections in the area (Langston, 1953; Romer, 1960). As a result of these collecting trips Romer (1937) described a new species of the pelycosaurian reptile *Sphenacodon*—*S. ferocior*—based on skull and anterior vertebrae, and Langston (1952) described a short string of vertebrae with ribs of an embolomorous amphibian, the first record for the state, that may be assignable to *Archeria*. Both species, as well as the remains of a large diadectid amphibian, probably *Diadectes*, were collected at the abandoned Spanish Queen mine locality. Further, about 100 m north of this site vertebrae of a rhachitomous amphibian, probably *Eryops*, an embolomorous vertebra, and various skeletal elements of small diadectids and sphenacodonts were collected from a small bone bed, the Johnson locality (Langston, 1953). In the 1970's Berman made several collecting trips to the Jemez Springs area. Although collections were made throughout the extent of the Jemez Springs Abo exposures, the only significant find described was the partial skeleton of the pelycosaurian reptile *Dimetrodon*, which was made the basis of a new species, *D. occidentalis* (Berman, 1977). In addition to *Trimerorhachis sandovalensis*, other faunal elements from the Abo beds of Jemez Springs can

be reported here for the first time: the freshwater shark *Xenacanthus* (a tooth, CM 38026), the lungfish *Gnathorhiza* (tooth plates, YPM 8636 and YPM 8637), and the amphibians *Platyhystrix* (neural spine fragments, CM 32029) and *Diplocaulus* (a vertebra, CM 38028). On the basis of these recent finds, it can now be stated that the faunal assemblage from the Jemez Springs area is typical for the Abo Formation throughout its wide extent in New Mexico (Olson and Vaughn, 1970). The one taxon of the Abo fauna known only from the Jemez Springs area, an embolomorous amphibian (Langston, 1952, 1953), can now be reported from a second Abo site farther south in the state. Numerous embolomorous vertebrae (CM 38031), most of which are articulated in short strings of two or three obviously belonging to a single individual, were collected from a probable pond deposit in the Abo exposures along the eastern margin of Sierra Lucero, Valencia County, southeast of Albuquerque.

Recent studies of the Lower Permian localities of New Mexico have shown that there are significant differences between the faunas of the Abo Formation exposed at Jemez Springs and those of the Cutler Formation exposed only about 45 km to the north near Arroyo de Agua and about 60 km to the northeast in El Cobre Canyon. The Arroyo de Agua area has been intensively prospected and the vertebrate collections it has yielded are unequaled elsewhere in New Mexico. Excellent summary discussions of the Early Permian vertebrate faunas of this region, as well as those from other regions of the state, are given by Langston (1953) and Romer (1960). In addition, the former includes a detailed account of the amphibians of New Mexico known at that time. Although all three areas contain many elements in common, there are several notable examples of animals known from Jemez Springs, and for that matter the Abo beds of the entire state, that are absent from the Arroyo de Agua and El Cobre Canyon areas. These include the lungfish *Gnathorhiza*, the amphibians *Diplocaulus*, *Trimororhachis*, and an embolomere that may be referable to *Archeria*, and the reptile *Dimetrodon*. Numerous genera are present at Arroyo de Agua but not at Jemez Springs, or any other Abo area—the amphibians *Pantylus*, *Zatrachys*, *Chenoprosopus*, *Ecolsonia* (Langston, 1953; Vaughn, 1969c), and *Tseajaia* (here reported for the first time from New Mexico on the basis of a nearly complete skeleton, CM 38033), the cotylosaur *Limnosceloides* (Langston, 1966), and the reptiles *Aerosaurus* and *Oedaleops* (Langston, 1965). *Tseajaia* is otherwise known only from the Lower Permian Organ Rock Shale, Cutler Group, of southeastern Utah (Vaughn, 1964a; Moss, 1972). Although the El Cobre Canyon fauna is less diverse (that is, less well known) than that of Arroyo de Agua, both are, with some exceptions, similar (Vaughn, 1963). To date, five genera, *Chamasaurus*, *Limnoscelis*,

Diasparactus, *Baldwinonius*, and *Nitosaurus* have been named that are only found in El Cobre Canyon. *Limnoscelis paludis* and *Diasparactus zenos*, however, have close counterparts in the cotylosaurs *Limnosceloides brachycoles* and *Diadectes lentus* of Arroyo de Agua. The pelycosaurian reptiles *Baldwinonius* and *Nitosaurus* and the primitive reptile *Chamasaurus* are known from very fragmentary specimens and their determinations have to be considered questionable until better specimens are found.

No clear explanation can be offered to explain the differences between the faunal assemblages of the Jemez Springs, Arroyo de Agua, and El Cobre Canyon areas. The red-bed deposits of all three areas, though not continuous in outcrop, were undoubtedly derived from the same source, the Uncompahgre highland to the north and northeast, and their fossiliferous levels are essentially equivalent in age, middle to late Wolfcampian (earliest Permian) age (Langston, 1953; Romer, 1960), though this age assignment is far less certain for El Cobre Canyon (Vaughn, 1963). Formational distinction between the Abo and Cutler beds in northwestern New Mexico was made by Northrop and Wood (1946) on the basis that the Abo intertongues with the overlying Yeso Formation of Lower Permian age, whereas the Yeso is not distinguishable from the Cutler. They have drawn, somewhat arbitrarily, the boundary between the Abo to the south and Cutler to the north at 36°N latitude. No major barriers, such as a mountain chain, can be invoked to explain the marked faunal differences between the spatially close faunas of Jemez Springs and Arroyo de Agua. Differences in the Early Permian depositional environments of Jemez Springs, Arroyo de Agua, and El Cobre Canyon areas are suggested by subtle differences in their sediments. The Lower Permian sections of Jemez Springs and Arroyo de Agua are dominated by bright red and chocolate-brown sediments. The majority of vertebrate fossils at Arroyo de Agua are, however, closely associated with extensive pond or lake deposits that are characterized by thick sequences of variegated mudstones (Langston, 1953), whereas at Jemez Springs pond or lake deposits of the kind found at Arroyo de Agua are absent and fossils are most often associated with stream-channel deposits. Vertebrates from El Cobre Canyon are mainly associated with chocolate-brown conglomerates and purple to light gray mudstones; bright red sediments are far less evident.

In recent years Vaughn (1966*b*, 1969*b*, 1970) has offered a tentative hypothesis to explain the distributional patterns of certain vertebrates during the Early Permian over the southwestern United States as a whole. He draws a distinction between "truly deltaic" and "somewhat more upland" environments based primarily on paleogeographic reconstructions of positive elements and seaways. "Truly deltaic" is

applied to areas found near the borders of persistent seaways and whose faunas included as "marker" elements rhipidistian crossopterygian fishes, the amphibians *Diplocaulus* and *Seymouria*, and the reptile *Dimetrodon*. "Somewhat more upland" denotes areas far removed from seaways and close to margins of positive elements and lacking the above deltaic marker animals. Applying these criteria, Vaughn designates the Jemez Springs, Arroyo de Agua, and El Cobre Canyon areas as all representing "somewhat more upland" environments.

In order to test Vaughn's hypothesis it is necessary to describe briefly the paleogeographic setting of New Mexico during the Early Permian. Fig. 9 is an attempt to present the broad paleogeographic features of New Mexico during early Wolfcampian time; it is compiled from various sources (Baars, 1962; Hills, 1963; Kottlowksi, 1963; McKee et al., 1967; Kottlowksi and Stewart, 1970), not all of which agree in detail on the extent of the various positive elements. From the same sources it is also possible, and indeed important here, to describe briefly the major physiographic changes that occurred in New Mexico during Wolfcampian time. During early Wolfcampian time vast floods of eroded siliciclastics, derived from the positive elements in New Mexico and adjoining areas of Arizona and Colorado, filled remnant Pennsylvanian basins. The Row-Mora basin of northeastern New Mexico received the red-bed sediments of the Sangre de Cristo Formation from surrounding highlands. Vertebrate fossils from the Sangre de Cristo southeast of Santa Fe in Santa Fe and San Miguel Counties indicate a Wolfcampian age (Langston, 1953; Olson and Vaughn, 1970); disjunct exposures in south-central Colorado, however, extend down into the Upper Pennsylvanian (Vaughn, 1969a, 1972). In early Wolfcampian time the clastic wedges of the Abo and Cutler Formations extended as coastal plains bordering shallow marine environments; only two such areas are important to the discussion here. In central and south-central New Mexico Abo red beds interfinger with marine carbonates of the northward extension of the Hueco Formation into the Orogrande Basin, forming a mappable, transitional unit, the Bursum Formation. Along the southeastern border of the Orogrande Basin in Otero County, Otte (1959) renamed the Bursum as the Laborcita Formation. Near-shore conditions also existed at this time in the southeast corner of Utah in San Juan County. Here the red-bed sediments of the Halgaito Shale, a westward extension of the lowermost levels of the undifferentiated Cutler red beds along the western margin of the Uncompahgre highland, interfinger northward with marine carbonates of the Elephant Canyon Formation. By late Wolfcampian time the Elephant Canyon embayment had regressed northward, well away from the region of concern here. During the Wolfcampian vast amount of Abo detritus derived mainly from the Uncompahgre

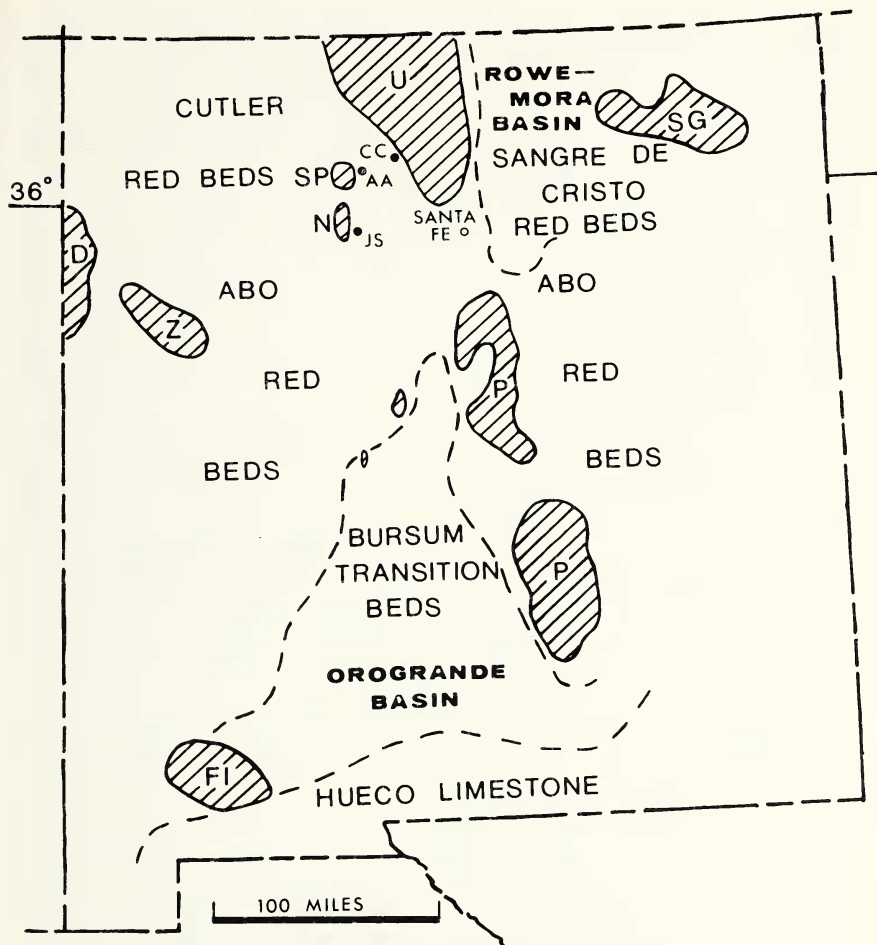


Fig. 9.—Generalized map showing broad paleogeographic features of New Mexico during early Wolfcampian Permian time. Positive areas indicated by oblique ruling: D, Defiance; FI, Florida Islands; N, Nacimiento; P, Pedernal; SP, San Pedro; SG, Sierra Grande; U, Uncompahgre; Z, Zuni. Wolfcampian vertebrate collecting areas Jemez Springs (JS), Arroyo de Agua (AA), and El Cobre Canyon (CC) indicated as closed circles. Map compiled from Baars (1962), Hills (1963), Kottlowski (1963), McKee et al. (1967), and Kottlowski and Stewart (1970).

highland of northern New Mexico and southern Colorado were carried southward as fluvially transported sediments, forming an advancing coastal plain. By the end of the Wolfcampian the northern derived red beds had buried the Zuni, Defiance, Nacimiento-San Pedro, and much of the Pedernal positive elements. This episode also resulted in the

retreat and burial of the Bursum Formation by the Abo red beds, pushing the shoreline within the Orogrande Basin southward to only 60 or 80 km north of the New Mexico-Texas border. These events created a broad mesic coastal plain with relatively little relief (Baars, 1962) that extended from the southern end of the Uncompahgre highland to the Bursum shoreline, a distance over 300 km.

Vaughn plotted the distributions of his "truly deltaic" and "somewhat more upland" faunas on a paleogeographic map that depicted an early Wolfcampian topography comparable in great part to that shown in Fig. 9. The majority of the Early Permian faunas of New Mexico, however, are believed to be middle to late Wolfcampian in age. As discussed above, the topography at this time had been altered greatly from that of the early Wolfcampian. In late Wolfcampian time the seaway nearest the Jemez Springs fauna was that occupying the Orogrande Basin. At this time, however, the northernmost margin of the Orogrande seaway, as represented by the Bursum Formation, had retreated a considerable distance southward from its narrow extension into central New Mexico, and the Jemez Springs fauna may have been as much as 300 km north of the Bursum strand line. The discovery of a partial skeleton of *Dimetrodon*, one of Vaughn's "truly deltaic" markers, in the Abo Formation of the Jemez Springs area (Berman, 1977) is an important contradiction to Vaughn's hypothesis. Subsequent to that report, *Dimetrodon* has been found to be a rather common element of the Abo fauna of Jemez Springs. The presence of *Diplocaulus* in the Jemez Springs area is also unexpected according to Vaughn's hypothesis. Yet, the absence of rhipidistian crossopterygian fishes and *Seymouria* might be viewed as negative evidence in support of Vaughn's analysis; this might be especially valid for the former. West of the midcontinental states of Texas and Oklahoma *Seymouria* is known only from the Organ Rock Shale, Cutler Group, of southeastern Utah (Vaughn, 1966a). Rhipidistian fishes, on the other hand, have been reported in the far Southwest from the Laborcita (=Bursum) Formation of south-central New Mexico (Vaughn, 1969b) and the Halgaito Shale, Cutler Group, of southeastern Utah (Vaughn, 1962; Thomson and Vaughn, 1968); both areas apparently closely bordered seaways. If rhipidistian fishes were at all abundant in the Jemez Springs area during the Early Permian, there seems a good chance that at least their heavily built and easily recognized scales would have persisted and should be found. These occurrences of rhipidistians, particularly when viewed in light of their apparent absence from Jemez Springs and other red-bed deposits distant from areas of interbedding with marine carbonates, may indicate a distribution pattern that was restricted to margins of seaways. It is important to note here that Vaughn also tentatively designated the Sangre de Cristo Formation

southeast of Santa Fe as representing a "somewhat more upland" environment. This assignment was based not only on reconstruction of paleogeographic features, but apparently on the absence of "truly deltaic" markers. A fairly large, as yet undescribed, collection of vertebrate fossils has recently been made in this area by Berman, providing a faunal list that includes *Diplocaulus*, but equally important lacks elements to suggest any special affinities with the "somewhat more upland" faunas of Arroyo de Agua or El Cobre Canyon. It therefore appears that the only examples of Vaughn's "somewhat more upland" faunas in New Mexico are those of Arroyo de Agua and El Cobre Canyon. Both areas are close to the southern portion of the Uncompahgre highland (often indicated separately as the San Luis uplift) which undoubtedly persisted as a prominent topographic feature during Wolfcampian time—its erosional deterioration accounting for most of the sediments that buried, or nearly buried, the other positive elements of the state. It would therefore seem that Vaughn's "somewhat more upland" faunas were much more restricted, at least in New Mexico, than originally suggested by him.

Recent discoveries also raise the possibility that Vaughn's "truly deltaic" fauna should also include *Trimerorhachis* and *Gnathorhiza*. Both genera occur in widely scattered localities that extend from southeastern Utah to south-central New Mexico and in coastal plain deposits that cannot all be considered to have formed near the borders of persistent seaways. In addition to the type skull of *Trimerorhachis sandovalensis*, six specifically indeterminate skulls of *Trimerorhachis* are now known from the Abo Formation of New Mexico—the greater part of a skull from the Caballo Mountains in Sierra County (Olson and Vaughn, 1970); two nearly complete skulls (CM 38032 and CM 26563), as well as several skull fragments, from a freshwater pond deposit in Los Pinos Mountains in Socorro County; a nearly complete skull (CM 38030) from the probable pond deposit on the eastern margin of Sierra Lucero in Valencia County from which also came the embolomorous vertebrae (CM 38032) mentioned earlier; a partial skull with postcranial elements (CM 38027) from a stream-channel deposit in the Jemez Springs area. In addition to the *Gnathorhiza* tooth plates already noted from Jemez Springs, Vaughn has reported *Gnathorhiza* tooth plates from the Halgaito Shale and from equivalent strata low in the undifferentiated Cutler in San Juan County, southeastern Utah (Vaughn, 1969b; Olson and Vaughn, 1970), as well as what are probably aestivation burrows of *Gnathorhiza* in the Sangre de Cristo Formation in San Miguel County, New Mexico (Vaughn, 1964b). Berman (1976, 1979) has recorded this genus from three localities in New Mexico, two of which are the same as those given above for *Trimerorhachis*—numerous articulated specimens preserved in aestivation

burrows in the Abo pond deposit in Los Pinos Mountains, Socorro County, that yielded two skulls and skull fragments of *Trimerorhachis*; two tooth plates from the probable Abo pond deposit east of Sierra Lucero, Valencia County, that yielded a single skull of *Trimerorhachis*; two tooth plates from a stream channel lens in the Sangre de Cristo Formation, San Miguel County, that is only a few kilometers from the probable *Gnathorhiza* burrow locality described by Vaughn (1964b). The addition of *Gnathorhiza* and *Trimerorhachis* to Vaughn's "truly deltaic" markers should not be unexpected, because they are typically found in close association with *Dimetrodon*, *Diplocaulus*, and rhipidistian fishes in the classical Lower Permian terrestrial beds of north-central Texas.

In summary, it appears that Vaughn's Early Permian "truly deltaic" fauna (with the possible exception of the rhipidistian fishes), as well as *Trimerorhachis* and *Gnathorhiza*, had a distribution in New Mexico that not only included areas closely bordering seaways, but also extended well inland across a coastal plain to the margins of highlands. During middle and late Wolfcampian time, the age of most Permian vertebrate-bearing horizons in New Mexico, this coastal plain may have reached over 300 km inland. Though deltas almost certainly made up a part of the coastal plain, they undoubtedly represented only one of several types of habitats. Until thorough sedimentological study of the New Mexico red beds allows recognition of the various physical habitats, investigation of their possible role in vertebrate distributions should be postponed. We also recommend that the term "truly deltaic" is inappropriate to designate the now broadly definable lowland fauna and habitat, and should be replaced by a more general, physiographic term, such as "coastal plain." The above discussion should also not be interpreted as a total rejection of Vaughn's hypothesis. The distinction between "coastal plain" and "somewhat more upland" faunas may be valid. It is conceivable that the faunal differences between Jemez Springs, Arroyo de Agua, and El Cobre Canyon may reflect an ecological sampling along a transect that extended from the inland margin of the mesic "coastal plain" up onto the higher slopes of the Uncompahgre highland where Vaughn (1970) suspects conditions may have been wetter and cooler. The absence of rhipidistian fishes and *Seymouria* from the Jemez Springs area might be viewed as negative evidence of its marginal position within the coastal lowland habitat. It also seems reasonable to speculate that the unusual adaptation of *Gnathorhiza* to aestivate in apparent response to marked dry seasons may have provided them with a competitive advantage that favored habitation of the more arid coastal lowlands but not the upland areas. Along this same line, it is interesting to note Olson's (1958, 1977) observation that *Diplocaulus* and *Trimerorhachis* may have been

aestivators, at least in early stages of life; at any rate, he contends that they were clearly capable of surviving severe drying conditions even as adults.

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